

## Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.





# YELLOW DWARF

*A Problem Disease of Small Grains*

ARS 22-70



*Growth Through Agricultural Progress*

June 1961

---

Agricultural Research Service  
UNITED STATES DEPARTMENT OF AGRICULTURE

## TO THE READER:

This Special Report has been written as a compact account of a virus disease of small grains that is widespread in the United States and a serious problem for farmers. The report is supplied to agricultural leaders as a basis for answering routine queries on this "yellow dwarf" disease and what may be done to combat it, and for developing programs on behalf of growers of small grains and forages where the disease is destructive.

# YELLOW DWARF--A PROBLEM DISEASE OF SMALL GRAINS<sup>1</sup>

A virus-caused "yellow dwarf" type of disease that attacks small-grain and other grass plants has been rolling up evidence that it is a costly crop destroyer, and a hard one to fight.

In United States farming areas, the virus--spread by aphids--has been outstandingly destructive to oats, secondarily to barley. Wheat, rye, and many pasture and range grasses can be infected.

Only in recent years has research been able to make solid progress toward understanding and combating this yellow dwarf disease.

For oat growers and many other farmers, some of the new-found information is important for knowing what the disease is like and what protective measures are available or in prospect.

Yellow dwarf has many extraordinary features.

## The Economic Threat

The virus responsible for yellow dwarf was discovered in 1951 and identified as the cause of varied plant symptoms. Since then, scientists have become convinced that the virus made trouble for farmers long before 1951. Old records fit neatly with what has been learned about the virus at work.

Yellow dwarf almost certainly was the "mysterious disease" described as a browning or blight that took alarming toll of oat crops as far back as 1889 and 1890. It was the oat disease that New York and Ohio Valley growers in 1907 called red leaf because their stricken oat fields were heavily patched with red. It was the disease that caused barley to be stunted and turn brilliant yellow in California in 1947 and again in 1951, so that it was called barley yellow dwarf. The virus, working these and other color effects, undoubtedly has harried farmers in more times and places than agricultural history will ever disclose.

Recently, 1959 was a "yellow dwarf year" when the disease was recognized in 22 States, and rampant in the Midwest where four-fifths of United States oats are grown. Oat losses from this epidemic were estimated in a number of States, notably: Missouri, 37 percent; Illinois, 28 percent; Indiana, 27 percent; Kansas, 25 percent; Iowa, 12 percent; Oregon's Willamette Valley, 32 percent. Many oat fields were so badly damaged that they were plowed up and replanted, or left unharvested. Putting evidence together, observers judge that the epidemic cut the United States oat crop of 1959 by 10 to 15 percent. Barley was damaged more than oats in a few States in 1959, and wheat was damaged in a few

<sup>1</sup> Scientists most commonly call the disease barley yellow dwarf because the virus causing it was discovered in barley and named barley yellow dwarf virus. Informally, the full name of the disease is sometimes shortened to yellow dwarf--when it is clear that yellow dwarf of grass family plants is meant. It is always important to avoid confusion with yellow dwarf diseases, due to quite different causes, that attack vegetables and some other types of crops.

localities. In appraising the epidemic outcome, many observers emphasized that they could not clearly distinguish and exclude losses due to direct aphid feeding. Some efforts were made to appraise the destructiveness of the virus alone, and these indicated that the virus caused the bulk of the damage.

In 1960, there was a conspicuous outbreak of the same disease in Northeastern States and Ontario, Canada. In the United States, from Maine to Maryland wherever oat fields were hit by the epidemic, the loss in expected yield ranged from 10 to 50 percent.

No oat variety commercially grown has shown strong resistance to the virus, although some varieties have been less damaged than others. In barley, the disease is rated less serious than in oats, not because barley is less damaged, but because outbreaks in barley have been less frequent. Although wheat and rye can be infected, they have not seemed preferred feeding plants for aphids that spread the virus, and these grains may be less susceptible than barley and oats.

Looking backward, spectacular outbreaks of yellow dwarf seem to have averaged only about one in 10 years. This is informative, but not a guide to the future. Populations of aphids that spread the disease may vary from year to year. Moreover, the virus evidently is to blame for damage in years between epidemics. In 22 New York counties, oatfields have been surveyed 4 successive years, and not an oatfield was found free of symptoms.

Countries over the world are looking for the disease in their grain-fields and finding it. It is known to have been in Germany since 1932 at least. Since 1955, virus and aphid tests have proved that the disease is in Belgium, the Netherlands, Great Britain, Norway, Sweden, Finland, and New South Wales. And other parts of the world have reported finding the symptoms. One ARS scientist has called yellow dwarf the world's most widely distributed virus disease of grains. He commented: "The unusual thing would be to find a small grain area where the disease did not occur."

## The Complex Problem

Few diseases have ever posed a more complicated problem for research to unravel and for farmers to fight than this one.

At least 9 kinds of aphids that prey on grains and other grasses can spread the virus by taking it into their bodies when they feed on infected plants and transferring it to other plants during subsequent feeding. Aphids, wind-borne, can spread the virus hundreds of miles.

Nearly a hundred grasses besides grains can serve as host plants in which the virus may survive awaiting transport. Some show symptoms indicating damage, whereas others show none.

The virus itself has a complex character. Its strains range from mild to virulent, and the strains also differ in some way recognizable to aphids. In some cases, at least, an aphid species "specializes" in a strain that it can transmit.

## Facing up to the Problem

Concern over this virus and its destructiveness is attested by more than 200 research reports published since its discovery. Most of the research has been done in the United States and Canada where the virus has been conspicuously active.

After 10 years of knowing the virus, the situation has several encouraging aspects:

- Crop research specialists have made a start toward protection, primarily by breeding varieties that are more productive under the virus' attack than varieties currently grown for crops. Some relatively resistant varieties are available and others are in prospect.
- An important outcome of studying yellow dwarf may be to upgrade ideas of what a good oat crop is. The disease unrecognized may account for many oat stands that perplex growers because the start is favorable and then small to large groups of plants look malnourished and yield below expectation. A determined fight on the disease with the best-adapted varieties, and other tactics as these become available, could overcome a drag on quality and quantity of oat yields--not only in yellow dwarf years, but every year.
- So much has been learned about this disease that, while gaps remain, the picture is clear enough to give sound guidelines for continued research, and some precautionary measures for growers.

Following sections of this report enlarge on significant points that have been outlined briefly. Included are some details of research done by the Agricultural Research Service of the U. S. Department of Agriculture and cooperating State Agricultural Experiment Stations. ARS scientists have made substantial contributions to understanding the disease and have developed some techniques for working with it. They are doing intensive work in breeding oat and barley varieties for higher resistance and have started similar work with wheat.

## HOW THE DISEASE AFFECTS PLANTS AND YIELDS

### Plant Symptoms

Yellow dwarf infection in grainfields, pastures, or weed grasses is often hard to diagnose, even for trained observers. Diagnosis is harder in autumn than spring because symptoms tend to be suppressed. The disease does display characteristic symptoms. Considered individually, the symptoms may be confused with malnutrition or other diseases or with aphid feeding damage. Combined symptoms, particularly in badly damaged plants, give reason to suspect yellow dwarf.

Stunting is the most consistent symptom in susceptible plants. Plants infected at seedling stage may be dwarfed to less than half normal height. Plants infected as late as heading stage are dwarfed slightly, if at all. Roots, as well as shoots, of young plants are stunted by the virus, particularly if moisture is scarce.

Discoloration is the most eye-catching symptom. It starts with pale streaks and may spread to entire leaf discolored. Infected rows or

patches of a crop, where virus-carrying aphids have fed, often show mass discoloration. The colorings vary but show some consistency with the kind of plant:

In barley--a brilliant yellow.

In oats, wheat, and rye--a faded green to dull yellow; however, foliage may turn bright red, ranging toward either orange or purple.

In forage and weed grasses--discoloration, if any, tends to be like that of oats, but many grasses show no signs of infection.

One difficulty in recognizing the disease is that foliage color symptoms may be altered by environmental conditions. Cool temperatures bring out the reddening in plants subject to this reaction. Very fertile soil sometimes brings out a dark greenness in infected plants, instead of the more characteristic colors. This darkening may appear when nitrogen in the soil is excessive from high fertilization or a preceding crop.

Leaf form sometimes shows serrated (toothed) edges. The cutting is occasionally deep enough to sever leaf tips. Leaves sometimes curl.

Blasted florets are a common symptom. Kernels that form often shrivel.

## Damage Consequences

Grain damage from the virus is most serious when it attacks young plants. It can kill plants in the early growth stage if they are of a highly susceptible variety and the virus a virulent strain. More commonly, young plants survive but many spikelets that develop fail to fill out with grain. Plants infected as late as heading stage escape radical damage but may not develop the full weight of their expected yield.

Foliage damaged by the virus may be a cause of loss to farmers who rely on the plants for forage. The discolored leaves are suspected of losing some nutrient values, although it is not yet known whether such losses are significant in foliage of grain or pasture grasses. British scientists recently tested infected wheat leaves for starch, and found it conspicuously present in contrast to normal low-starch content--a clue to the nature of the damage.

A great deal of winter damage of grains may be due, not to cold, but to yellow dwarf. As an exploratory test, ARS and Illinois Agricultural Experiment Station scientists in 1957-58 released aphids carrying the virus on caged plots of fall-planted seedlings. Three oat varieties and one barley variety were thus tested. Test plots were exposed to infection at three different stages of starting growth (October 21, November 7, and November 20).

About a third of the plants infected October 21, when seedlings were very young, did not survive the winter, and the surviving plants showed symptoms of yellow dwarf in April, and bore little grain. In plots infected November 20, when seedlings were a month older, a tenth or less of the plants were winterkilled, and their yields were somewhat better, although far below yields of check plots that were protected from infection and bore normal crops.

So variable are symptoms and damage consequences of yellow dwarf that, when the Illinois researchers continued exploratory work on fall-sown grains, they not only added new information but encountered some different effects. In 1959-60, they sought to compare effects of fall and spring infection in one variety each of oats, barley, and wheat. The oat plantings protected from fall infection were 100 percent killed by the cold that winter, so that none could be spring-infected. The uninfected barley and wheat survived 100 percent. Thus, the amount of cold gave a clear-cut basis for differentiating winter injury from virus damage.

Throughout fall growth, none of the three grains exposed to infection showed any symptoms, although the virus was found in plants. All fall-infected oats and barley were weakened and died in the winter. All fall-infected wheat survived. In late spring and summer, the fall-infected wheat showed one conspicuous symptom: Severe dwarfing that could be confused with many plant disorders or diseases. The wheat showed little or no foliage discoloration.

Meanwhile, some of the wheat and barley that had been protected from infection in fall was exposed to it in late April. This spring-infected grain, by contrast with the fall-infected, developed striking foliage symptoms and no severe dwarfing.

Yield tests indicated that the earlier the infection, the greater the grain loss. Compared with the normal yield of the uninfected wheat plants, those infected in mid-October had yield cut about two-thirds and those infected in late April had yield cut about half.

## DISCOVERY OF THE VIRUS

The virus remained undetected for a long time because it operated with some formidable advantages over man's agricultural experience. The symptoms it caused in infected plants were like disguises, suggesting separate diseases in different crops at different times. Agricultural workers sought causes among diverse conditions, from bad growing weather and soil deficiencies to a range of pests that included blight, rust, and insects. The nature of the disease, involving teamwork of a virus, aphids, and numerous grass family host plants, posed a problem unmatched in the known diseases of small grains. And apart from bad outbreaks, the disease usually was noticed only on scattered plants, where it was insignificant compared to evidences of well-known major diseases.

Detective skill of California scientists disclosed the virus when it attacked three kinds of grain in a spectacular display of destruction. In April 1951, California growers began reporting a stunting and yellowing in barley and a stunting with different color symptoms in oats and wheat particularly in late plantings of these two grains.

All evidence from the 3-crop damage indicated that it was due to the same cause, and two University of California scientists launched an intensive search for the unknown cause. They ruled out weather, soil conditions, and fungi, and then focused on aphids, which were unusually abundant.

Observing that barley was severely damaged even where the aphids were not feeding in especially thick hordes, they inferred that, if aphids

were responsible, they could be spreading a virus. Greenhouse experiments confirmed this deduction. Four species of aphids reared on naturally diseased barley and wheat did transmit the infective agent to healthy barley, wheat, and oats. The greenhouse test plants developed the same disease symptoms seen in grainfields. This evidence and many other findings from the California research put the study of the disease on a firm basis.

## TEAMWORK OF THE VIRUS, APHIDS, and HOST PLANTS

### Basic Information a Major Research Goal

Exploring the intricate operation of the disease is one of the most important objectives in the current research. Plant breeders in particular need this information as a guide to knowing which of their experimental selections are the most likely to withstand the disease in farming conditions. Entomologists and other agricultural specialists need basic information about the disease also, as a guide to additional means of combating the disease.

Information is accumulating on the intricate pattern by which the disease operates. An ARS plant pathologist stationed at Cornell University Experiment Station in New York is devoting intensive effort to basic study of the disease and has devised special techniques for this work.

For one test, he obtained more than 150 infected oat and barley leaves, each leaf sent from a different infected plant, and the whole collection representing 13 States. The purpose of the test was to pit 4 species of aphids against the virus from many farming localities and therefore very probably including more than one strain.

He cut the one-leaf samples each into four long strips, and laid each strip on moist filter paper in a dish provided with a tight cover. In every dish he placed virus-free aphids of a single species--apple grain, corn leaf, English grain, or greenbug. In the tight-covered dishes the aphids fed for 1 to 2 days, and they were then moved to feed on healthy oat seedlings in protected cages. These aphids showed a good deal of specialization in either succeeding to transmit the virus, or failing. The most significant finding was that three strains of the virus could be differentiated by these aphid species.

For other tests, the virus has been extracted from infected plant tissue in partially purified form, as trial material for aphids to inject into healthy plants. A difficulty here has been getting the aphids to feed on extracts. This has been accomplished at Cornell by the technique of membrane feeding, shown in figure 1. Liquid virus preparations, containing clarified juice from plants and a sugar solution, are poured into tubes and a membrane is sealed over each tube. The tubes are suspended membrane end down over feeding chambers containing aphids, so that the aphids cling to the membrane and feed upside down as they feed in a field clinging to the underside of a leaf. Only with leafhoppers has this kind of membrane feeding been successful in previous research. After 16 to 18 hours of membrane feeding, the aphids are transferred with a tiny brush to healthy test plants to show whether they can transmit the virus strain. Infected plants develop symptoms within 2 weeks.

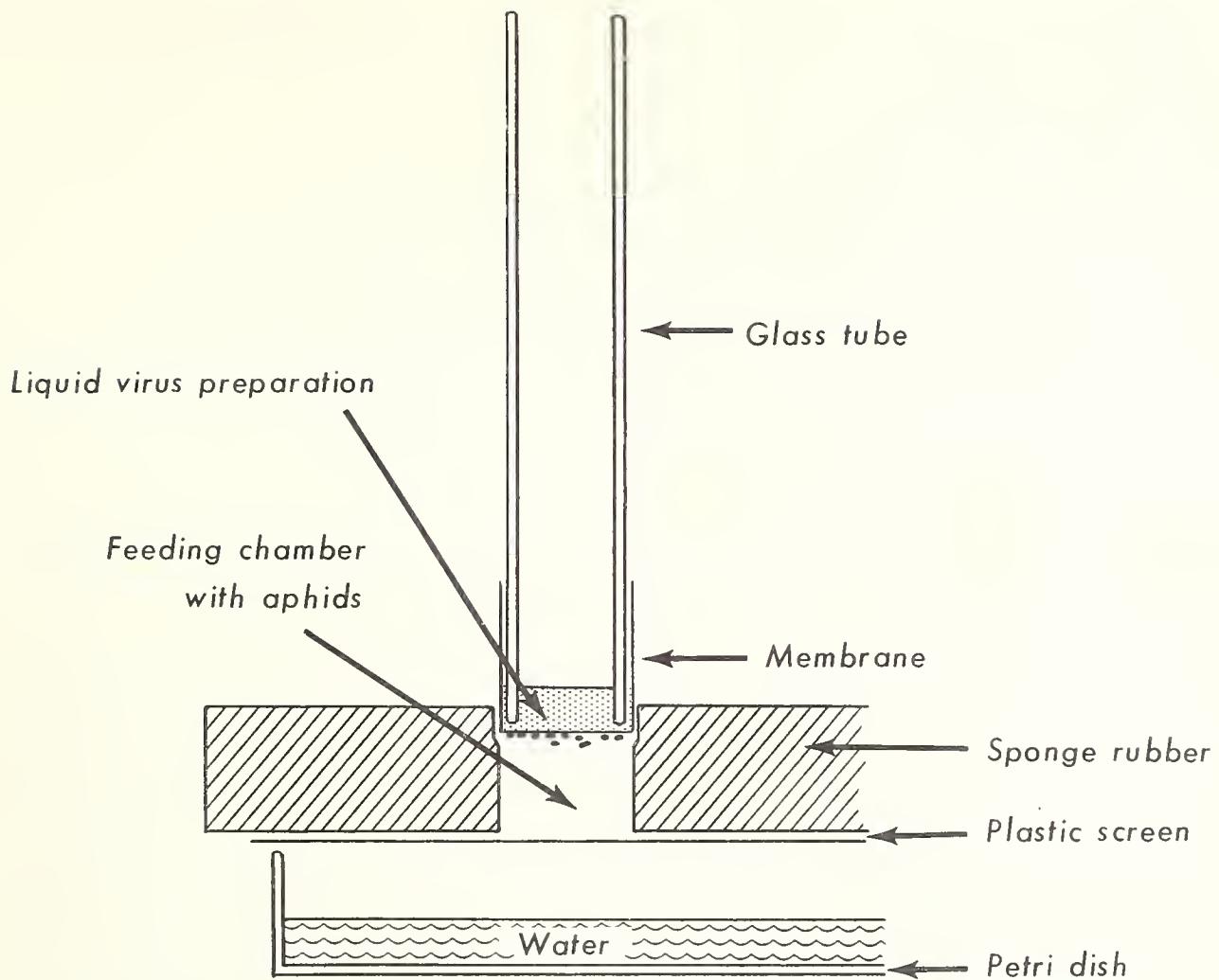


Figure 1.--The feeding tube in this diagrammatic drawing represents 1 of 6 such tubes suspended in round holes in a 6-inch square sheet of sponge rubber. Up to 20 aphids that have been starved a few hours are placed in each hole under a tube. The hungry aphids drive their feeding parts through the membrane to draw in the water-sugar-virus liquid, in a feeding manner that resembles their normal liking to feed upside-down, clinging to the underside of a leaf. Water in the petri dish serves several purposes, one being to keep the air moist for the aphids.

Because some aphids refuse membrane feeding, a way of injecting virus extract into them hypodermically has been devised. When expertly handled, a fine glass needle directed to a target point in the aphid's back between abdomen and thorax is effective. Ninety percent of Cornell aphids thus infected have survived to feed on healthy test plants and show which strains they could transmit.

Tests with partially purified virus extracts are the nearest that scientists have come to working with the virus itself. Efforts to isolate the virus from diseased plant material are now underway. Only when this important step has been achieved can research workers determine the chemical nature of the virus and learn how the strains differ. Knowing its chemical properties, they will have prospect of singling out the virus as an organism of recognizable size and shape. At present, it is undoubtedly visible in processed material from diseased plants, viewed under the powerful electron microscope, but it cannot be identified among other particles. Isolation of the virus is a preliminary step also to learning how

aphid species and plant hosts differ chemically or physiologically, in ways that account for their specialized association with the virus.

## Aphids Serving the Virus

Nine species of grain aphids have been found capable of spreading the yellow dwarf virus in United States research. And the list may lengthen.

Not all species of aphid vectors are of equal importance. The main vector may be different in epidemic years, and different in farming areas during the same epidemic. The apple grain aphid, for example, is known to have been a major vector of the virus in Washington and the English grain aphid in New York and other Northeastern States. The greenbug appeared to be the major vector in the Midwest in 1959.

There is no easy way of detecting those aphids that are vectors, nor even differentiating aphid species, in crop fields. Points, such as the following, about aphids in relation to the disease may be of interest to growers:

The virus is spread by aphids, and almost certainly in no other way. This has been established by many tests made in efforts to learn whether the virus has any other means of infecting plants. Plants are not infected from soil nor from seed--even when seed from infected plants are sown they produce uninfected and undamaged plants. All efforts to transmit the virus by injecting extracts into plants by hand have failed.

Aphids are "precision tools" for transmitting the virus. Their piercing-sucking mouth parts are adapted for feeding directly on the phloem--the vital food-conducting tissue of plants. It is in this phloem that the virus multiplies and starts its destructive action. Whether aphids also incubate the virus or are essential to it in some other developmental process has not yet been determined.

How thickly aphids infest a field is no dependable warning of a yellow dwarf outbreak. A devouring horde of aphids may include no virus vectors. A few vectors, alone or as a minor type in a heavy aphid infestation, are enough to spread the virus, if they feed actively, moving from plant to plant.

Aphids are born free of the virus. Once they take it in from a host plant, they may continue to transmit it to plants throughout a lifetime of feeding, or up to 2 to 3 weeks.

Symptoms of the disease in grain plants usually do not begin to appear until 2 to 3 weeks after aphid feeding, by which time the aphids that brought the virus have died.

Where aphids will take the virus is not predictable. Minnesota oat damage in 1959 apparently was due to aphids wind-borne from Kansas and Oklahoma. The aphid vectors remained air-borne 500 miles nonstop, judging by combined evidence: The same aphid species in both places, the lack of damage along the wind's northward sweep, the time of Minnesota's outbreak, and weather observations. (A cold front met and blocked the wind in the Minnesota area, so that aphids were dropped.)

## Host Plants of the Virus

Kinds.--More than 80 plants of the grass family have proved able to harbor the virus. Naturally infective grass plants from which it can spread include weeds and wild grains as well as pasture and range grasses and grain crops.

Corn and rice have been added to grains that scientists have infected with the virus in artificial conditions of caging greenhouse test plants and introducing aphids inoculated with the virus. There is no evidence thus far that either corn or rice has been infected or endangered by the virus in actual farming. Present evidence on susceptibility of these grains rests on two research accounts: University of California scientists in 1957 reported that they had tried six strains of the barley yellow dwarf virus on seedlings of Golden Bantam corn, and one strain induced symptoms of yellow dwarf. British scientists at Rothamsted Experimental Station in 1960 reported that they included a British variety of corn and one experimental rice selection among 40 test plants to be exposed to a virulent strain of the virus, and the corn and rice test plants developed characteristic symptoms.

Among the numerous hosts of the virus, some can be victimized by severe or lesser damage, whereas others provide lodging but remain symptomless. Symptomless hosts include annual ryegrass, Bermudagrass, Kentucky bluegrasses, orchardgrass, sweet vernalgrass.

Reservoirs of winter survival.--Especially important for the disease are perennial and fall-sown grass plants that can become reservoirs in which the virus overwinters and perpetuates itself. In eastern Ontario, research scientists in 1959 extracted the virus from overwintered wheat, winter rye, and some perennial grasses. They regarded their findings as evidence that winter reservoirs of the virus are common as far north as Canada, although they could not be sure whether Ontario's 1959 oat epidemic of yellow dwarf came mainly from local host plants or was brought by wind-borne aphids from some distance.

Palatability important.--Plants that offer preferred feeding for aphid vectors are the most significant in epidemic spread of the disease. Hungry aphids will feed on some unlikely plants if given no choice. But a species of aphids commonly feeds and multiplies on plants most palatable to its kind. Experiments have indicated a further reason why palatability is particularly important in a yellow dwarf outbreak: Vectors generally cannot become infective unless they feed half a day or longer on plants containing the virus.

## RESISTANT CROP VARIETIES THE MAIN DEFENSE

The best known strategy for dealing with barley yellow dwarf virus where it is destructive is to plant varieties that can withstand its attacks. Readyng these varieties is, therefore, an important phase of research on the disease.

This work has advanced furthest on oat and barley varieties. Work has started on wheat. Resistance in forage grasses has not yet received close attention, but if the virus parallels its grain damage with pasture and range damage, the selection, breeding, and widespread use of adapted grasses may become part of research efforts in dealing with yellow dwarf.

## Oats as an Example

Using oats as an example of this breeding work:

A basic step is to single out the more resistant among commercially grown oat varieties, and this is in progress. In the Midwest, for example, Putnam, Newton, and Tonka have shown an encouraging amount of resistance to yellow dwarf. These give Midwest oat growers some choice among present varieties.

To increase resistance, breeders are using the USDA World Oat Collection of more than 5,000 entries as source material. Seeds from this gene bank have already been planted in many oat-growing States. In each test several thousand entries are planted to try out all plants of any possible use.

In all of this testing, no oat plant of any part of the world has shown immunity to the virus. However, several wild, foreign-grown, or experimental types have shown high degrees of resistance, and such entries provide good breeding material for all parts of the United States. None of these more highly resistant oats is suited to our commercial production. Each has weak straw, low yield, susceptibility to other diseases, or some other undesirable character.

Breeders can use the resistant oats for initial crosses with more desirable oat types. It is then almost always necessary to follow with backcrossing of the hybrid to the desirable parent through one or more generations to strengthen desirable traits.

Oat breeding work to develop varieties with resistance to the virus has been started in a number of areas and has reached advanced stages in California, Illinois, and Indiana through cooperative work by ARS and State agricultural experiment stations.

The first improved oat variety specifically selected for resistance and released to commercial production in this breeding program is Curt, a red oat developed in California for Western use. It is considered outstanding for pasture, hay, and grain production, and has moderate resistance to yellow dwarf. Curt is shatter-resistant and rust-resistant for the West, although not adequately rust-resistant to serve the Midwest. Certified seed production began in 1959, so that seed would be ready for California growers in 1961.

The Illinois Agricultural Experiment Station, cooperating with ARS, has developed oat selections with five or more generations of backcrossing and has produced several selections considered promising. Seed of the selections have been made available to other oat breeders. If selections maintain their showing of resistance to the virus, they may be released for seed production in the next year or two.

## WHAT GROWERS CAN DO

Growers of small grains who find that they are taking losses from yellow dwarf are advised to consult with Extension workers, scientists at their State experiment stations, or other agricultural leaders in their State. In a good many States there is now useful information regarding the relative susceptibility of crop varieties currently grown in the area.

Growers can consider shifts to the more resistant of these varieties, if they have been planting the more susceptible varieties. And they can be on the lookout for new varieties with resistance, as these become available.

In addition, some protection can be given to small grain crops, mainly along the lines of normally good farming practices.

- Planting spring oats and other grains as early as weather permits is advised to give them a headstart before aphid season. Early spring sowing has long been recommended for escaping most grain diseases, and the yellow dwarf hazard is one more good reason for this practice. Aphids generally come along in a locality about the same time of year, regardless of crop stage. Early spring sowing will not prevent damage from the virus if aphids make an unusually early start, as they did in 1959. But in most years, it pays.

- Recommended rates for seeding serve best to protect grain plants from spread of the virus. Epidemics and experiments alike have demonstrated that yellow dwarf does less damage in solid stands than in sparsely planted stands. The thin stands allow aphid vectors to blow or fly freely from plant to plant. Planting should not be excessively close, because plants may lodge.

- Proper soil fertility and customary use of any insecticides that partially keep down aphids, and other management practices that are recommended for a crop in general, tend to lessen damage if the virus infects a field.

Not considered worthwhile is the destruction of small infestations of plants with yellow dwarf symptoms. By the time symptoms are evident, the aphid vectors usually have finished their work.

It is not generally worthwhile to plow up even a badly infected grain field if the field has been underseeded with a legume. Legumes are not subject to this virus, so that damage to the grain crop does not alter chances for a successful legume crop, and the grain plants themselves are likely to yield some usable grain or forage.

## RESEARCH TASKS AHEAD

Today's knowledge of the barley yellow dwarf virus indicates that it will be increasingly used as a test for selections developed in small-grain breeding.

Meanwhile, research specialists are aware of gaps in information about yellow dwarf that they need to fill in, to help breeders primarily, and also to help growers fight aphid vectors of the virus and protect crops by favorable management.

Goals ahead include learning--

- Whether crop varieties and experimental selections that resist one strain of the virus can be relied on to withstand other strains--and whether any one strain is a useful standard test.
- Whether virus strains differ from year to year and place to place, and, if so, what causes the difference.

- Whether aphid vectors merely provide transportation or are necessary to the virus in incubation or some other developmental stage.
- How the overwintering host plants are related to the development of the virus and its vectors.
- What temperatures or other winter conditions affect the survival or destruction of the virus or aphid vectors.
- What importance specific aphids have in spreading the disease.
- Whether it would be better to breed for resistance to the virus or for plants on which important aphid vectors will not feed.
- Whether aphid vectors can be killed with wholesale effectiveness by some systemic insecticide or other means than by presently known contact insecticides.
- What damage the virus does to seed production of forage grasses.
- Whether forage grasses infected lose much of their feed value, such as protein, carotene, or minerals.



